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A COMPARATIVE STUDY OF THE RESPIRATORY MUSCLES IN CHELONIA

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INTRODUCTION

The unique skeletal modifications in Chelonia have greatly influenced the morphological features of the soft parts in these animals. Of these modifications the rigid shell formation is the most prominent characteristic feature of the Chelonia; this has made their body wall immovable and hence the normal respiratory movements characteristic of amniotes are lost. This loss of active body wall movements has given much reason for discussion about the respiratory mechanism adapted by the chelonians, and from the time of Malpighi and Cuvier many attempts have been made to explain the phenomenon. Some have suggested that the throat movements similar to those seen in frogs are responsible for bringing about the expirations and inspirations in Chelonia; others have supposed that the movements of the limbs and the neck indirectly effect the expiration and inspiration. Recently McCutcheon (1943) has summarized the evidence that, on the contrary, the movements of certain abdominal muscles, the *diaphragmaticus*,¹ the *transversus abdominis*, the *serratus magnus* and the *obliquus abdominis*, bring

¹A matter of terminology must be mentioned here. McCutcheon (1943) described the flank cavity muscles in *Malaclemys centrata* where the *diaphragmaticus* muscle as described by him seems to be the same as the *muscularis striatum pulmonale* and quite different from the *diaphragmaticus* as described in this paper. Owen (1866), describing the musculature of *Emys europea*, describes the *diaphragmaticus* as formed of three parts originating from the carapace; two parts insert on the wall of the lung while the third one inserts on the plastron. This description compares well with the account given here, except that the two parts of the muscle described by Owen as inserting on the lung are here regarded as the *muscularis striatum pulmonale*, and only the third part which inserts on the plastron is the true *diaphragmaticus*.

about expiration and inspiration. He interprets the throat movements in *Chelonia* as functioning in olfaction and not in respiration. George and Shah (1954) have studied the respiratory mechanism in *Lissemys* and have confirmed McCutcheon's view that the abdominal muscles are effective for respiratory movements and that the throat movements are only for olfaction. In addition, they have also described the presence of an extra pair of muscles which cover the lungs completely in *Lissemys*. These muscles are composed of striated muscle fibres. On contraction of these muscles the pulmonary air is pushed out of the lungs, and on their relaxation the atmospheric air is taken in. Thus these lung muscles, the *muscularis striatum pulmonale*, aid the action of the abdominal muscles in bringing about the expiration and inspiration.

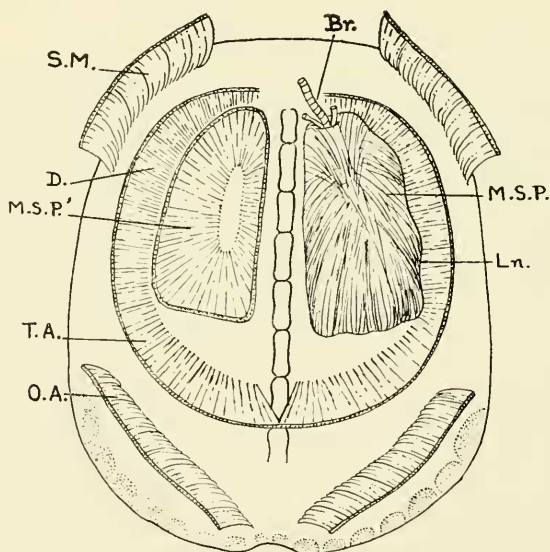


Fig. 1. Diagrammatic sketch of the disposition of the respiratory muscles in *Cyclanorbinæ* where the lungs are completely covered by the *muscularis striatum pulmonale*.

George and Shah (1955, 1958 and 1959) made a comparative study of the abdominal muscles and of the lung muscles in some additional chelonians: *Lissemys punctata* (all three

subspecies), *Geoemyda trijuga*, *Trionyx gangeticus*, *Testudo elegans*, *Malacochersus torneri* and *Eretmochelys imbricata*. According to their observations the lung muscle, the *muscularis striatum pulmonale*, covers the lungs completely in *Lissemys punctata*, partially in *Geoemyda*, while the muscle is totally absent in the rest of the forms they studied. Of the flank cavity muscles the *diaphragmaticus* and the *transversus abdominis* are

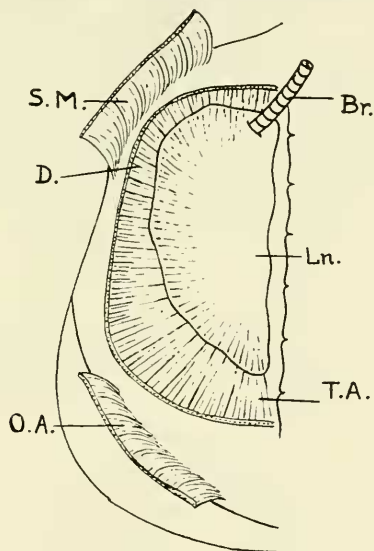


Fig. 2. Diagrammatic sketch of the disposition of the respiratory muscles in Trionychinae.

well developed in *Lissemys* and *Trionyx* where they join with each other to form a continuous muscle sheath covering the visceral organs including lungs. The *diaphragmaticus* in *Geoemyda trijuga* and *Eretmochelys imbricata* does not join with the *transversus abdominis* to form a continuous muscle sheath, but there is a bridge of connective tissue between them. In *Testudo elegans* and *Malacochersus torneri* the *diaphragmaticus* muscle is totally absent leaving only a thin membranous sheath of connective tissue in its place. The other flank cavity muscles, viz. the *serratus magnus* and the *obliquus abdominis* are present with slight variation in all the animals they studied.

In the light of these observations on the respiratory muscles in a very few chelonians, it was thought desirable to examine

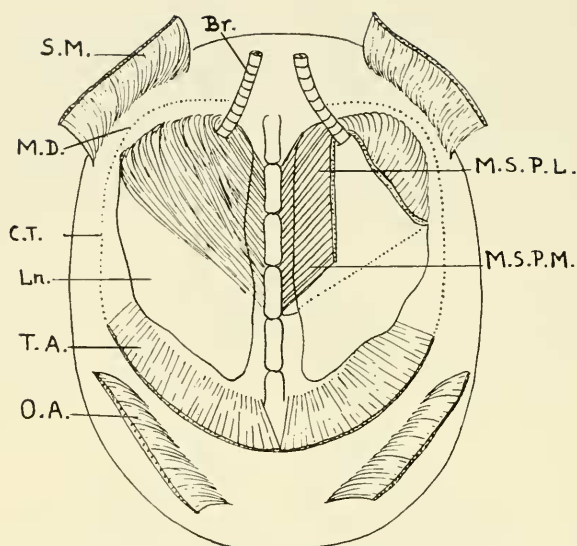


Fig. 3. Diagrammatic sketch of the disposition of the respiratory muscles in *Malaclemys terrapin terrapin*.

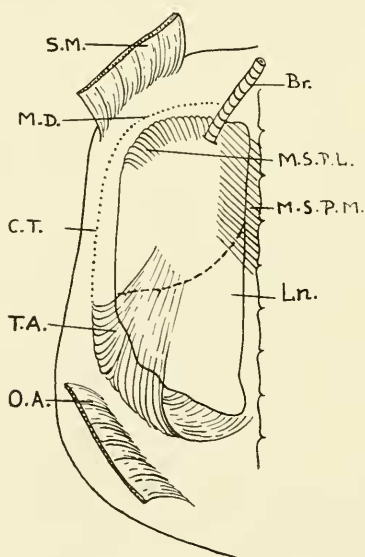


Fig. 4. Diagrammatic sketch of the disposition of the respiratory muscles in *Pseudemys floridana* and *Pseudemys texana*.

more forms representing, as far as possible, almost all the major groups of the order Chelonia, and make a comprehensive comparative study of these muscles to get an overall idea of the morphological features of the respiratory mechanism adapted by the animals of this order.

For this study some fifty different cryptodiran and nine pleurodiran forms were selected. A list of the animals chosen is given below.

This work was carried out at the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts, U.S.A. I am thankful to Dr. A. S. Romer, then Director of the Museum, and Dr. E. E. Williams, Curator of Herpetology, for all the facilities given and for their constant help and encouragement during the course of the study.

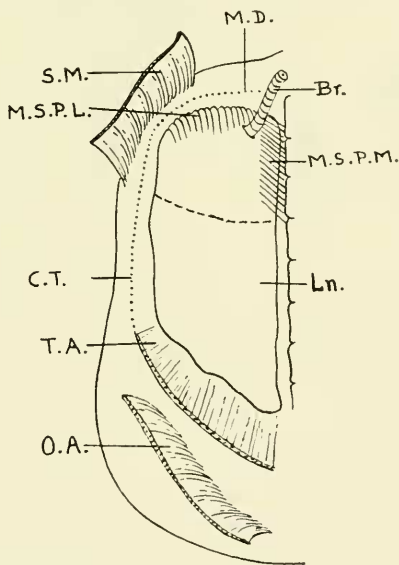


Fig. 5. Diagrammatic sketch of the disposition of the respiratory muscles in Emydinae forms in which the *diaphragmaticus* muscle is absent.

MATERIAL STUDIED

All the animals selected for the study were alcohol preserved and were found in excellent state of preservation. Careful dissections of the flank cavity muscles, the *diaphragmaticus*, the *transversus abdominis*, the *serratus magnus* and the *obliquus*

abdominis and the lung muscle, the *muscularis striatum pulmonale*, were done on these animals and following is the report of the comparative study.

List of chelonians selected for the present study:

CRYPTODIRA

TESTUDINOIDEA

TESTUDINIDAE

Emydinae

Chinemys reevesii
Chrysemys picta dorsalis
Chrysemys picta marginata
Chrysemys picta picta
Clemmys caspica caspica
Clemmys caspica leprosa
Clemmys guttata
Clemmys mutica
Cuora amboinensis
Deirochelys reticularia
Emydoidea blandingii
Emys orbicularis
Geoemyda manni
Geoemyda punctularia funerea
Geoemyda spinosa
Geoemyda trijuga
Graptemys kohni
Graptemys pseudogeographica
Kachuga tectum tectum
Malaclemys terrapin terrapin
Malayemys subtrijuga
Ocadia sinensis
Pseudemys floridana
Pseudemys texana
Terrapene yucatana

Testudininae

Geochelone pardalis
Pyxis arachnoides
Testudo graeca
Testudo hermanni
Testudo horsfieldii
Testudo kleinmanni

CHELYDRIDAE

Kinosterninae

Sternotherus carinatus minor
Sternotherus odoratus

Chelydrinae

Chelydra serpentina

TRIONYCHOIDEA

TRIONYCHIDAE

Cyclanorbinae

Cyclanorbis sp.
Cycloderma frenatum
Lissemys punctata
 (all three subspecies)

Trionychinae

Dogania subplana
Trionyx gangeticus
Trionyx sinensis
Trionyx triunguis

CHELONOIDEA

CHELONIDAE

Caretta caretta
Chelonia mydas
Eretmochelys imbricata
Lepidochelys olivacea

DERMOCHELYOIDEA

DERMOCHELYIDAE

Dermochelys coriacea

PLEURODIRA

PELOMEDUSIDAE

Pelomedusa subrufa subrufa
Pelusios subniger
Podocnemis expansa
Podocnemis lewyana
Podocnemis unifilis

CHELIDAE

Chelodina longicollis
Emydura krefti
Hydromedusa maximiliani
Phrynops geoffroana
Platemys platycephala

DESCRIPTION OF THE MUSCLES

Of all the respiratory muscles mentioned above, the lung muscle, the *muscularis striatum pulmonale*, shows the most extreme variation in Chelonia. It is so well developed in the forms belonging to the subfamily Cyclanorbinæ that it covers the lung completely while in the other subfamily, Trionychinae, the muscle is totally absent. In *Cyclanorbis* sp. and *Cycloderma frenatum* (Fig. 1) the muscle arises from the carapace in the vicinity of the second and third thoracic vertebrae and also from the lateral side of these vertebrae. The fibres arising from the carapace run over the entire dorsal surface of the lung and when they

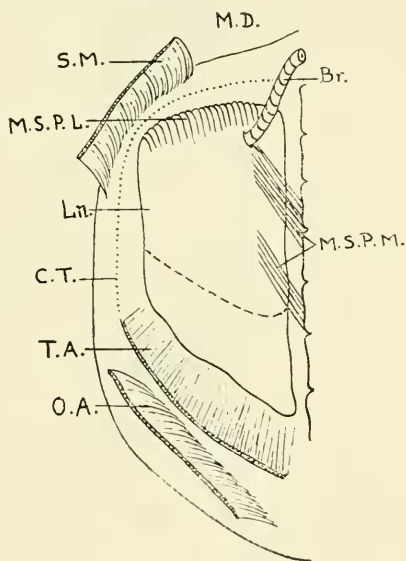


Fig. 6. Diagrammatic sketch of the disposition of the respiratory muscles in *Kachuga tectum*.

reach the outer, anterior, and the posterior limits of the lung they turn onto the ventral side and continue to run towards the entrance of the bronchus. The fibres arising from the lateral side of the thoracic vertebrae run over the medial side of the lung and then come onto the ventral side and reach the entrance of the bronchus. All the fibres of the muscle closely adhere to the wall of the lung. From the place of the origin of the fibres, the muscle could be arbitrarily divided into two parts, a lateral

part which arises from the carapace and a medial part which arises from the lateral side of the thoracic vertebrae. The *muscularis striatum pulmonale* in *Lissemys punctata* (Fig. 1) (George and Shah, 1954) differs slightly from the one in *Cyclanorbis* and *Cycloderma*; the muscle is otherwise very similar in its course and insertion in all the three genera of Cyclanorbinæ. In *Lissemys* the muscle arises entirely from the carapace and does not have its lateral part arising from the side of the vertebrae. The muscle in all the forms of the group Cyclanorbinæ is

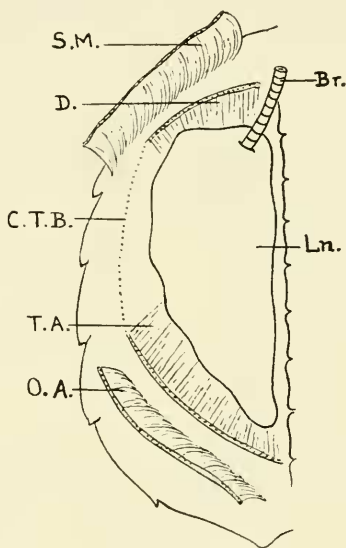


Fig. 7. Diagrammatic sketch of the disposition of the respiratory muscles in marine turtles.

innervated by the branches of the intercostal nerves. As said before, the muscle on its contraction pushes out the pulmonary air of the lungs, and on its relaxation the atmospheric air rushes in.

In *Trionyx gangeticus*, *Trionyx sinensis*, *Trionyx triunguis* and *Dogania subplana* (Fig. 2) belonging to Trionychinae, the *muscularis striatum pulmonale* muscles is totally absent.

All the forms belonging to the Emydinae have a *muscularis striatum pulmonale* which partly covers the lung. In this group the muscle shows great variation in different species.

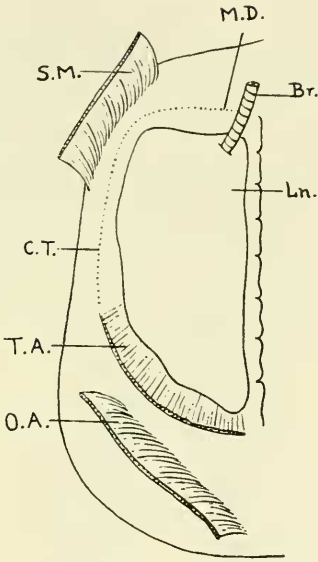


Fig. 8. Diagrammatic sketch of the disposition of the respiratory muscles in Testudininae, except *Pyxis arachnoides*.

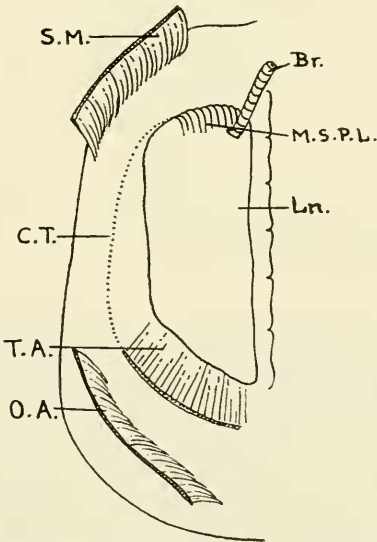


Fig. 9. Diagrammatic sketch of the disposition of the respiratory muscles in *Pyxis arachnoides*.

In *Malaclemys terrapin terrapin*, *Clemmys caspica caspica*, *Clemmys guttata*, *Graptemys pseudogeographica*, *Graptemys kohli*, *Cuora amboinensis*, *Pseudemys floridana* and *Pseudemys texana*, the *muscularis striatum pulmonale*, though only partly covering the lung, is well developed compared to other Emydinae. In these emydines the medial part of the muscle arising from the side of the thoracic vertebrae is well developed and quite extensive, while the lateral part of the muscle with its origin from the carapace, though well developed, is comparatively small

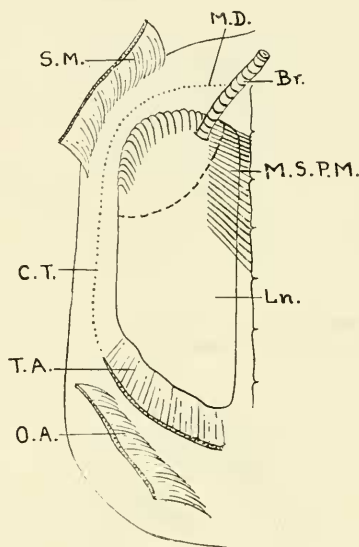


Fig. 10. Diagrammatic sketch of the disposition of the respiratory muscles in Pleurodira forms in which the *muscularis striatum pulmonale* is partial and the *diaphragmaticus* muscle is absent.

in extent. However, in *Malaclemys terrapin terrapin*, *Graptemys pseudogeographica* and *Graptemys kohli* the lateral part of the muscle is comparatively more developed than in the other emydines listed above. The place of origin of the lateral part of the muscle in these three forms is parallel to that of the medial part of the muscle (Fig. 3). In *Pseudemys floridana* and *Pseudemys texana* the place of origin of the lateral part of the muscle is perpendicular to that of the medial part of the muscle (Fig. 4).

In *Emys orbicularis*, *Kachuga tectum tectum*, *Ocadia sinensis*, *Chrysemys picta picta*, *Chrysemys picta dorsalis*, *Chrysemys picta marginata*, *Deirochelys reticularia*, *Emydoida blandingii*, *Clemmys mutica*, *Chinemys reevesii*, *Malayemys subtrijuga*, *Geoemyda punctularia funerea* (Figs. 5 and 6), *Geoemyda manni*, *Geoemyda spinosa*, and *Geoemyda trijuga* (Fig. 12) the medial part of the *muscularis striatum pulmonale* is very poorly developed and only covers a very small portion of the anterior medial side of the lung. The lateral part of the muscle is also less developed compared to that of *Malaclemys* and others and shows variations in its extent, never covering more than a small portion of the anterior and anterolateral side of the lung.

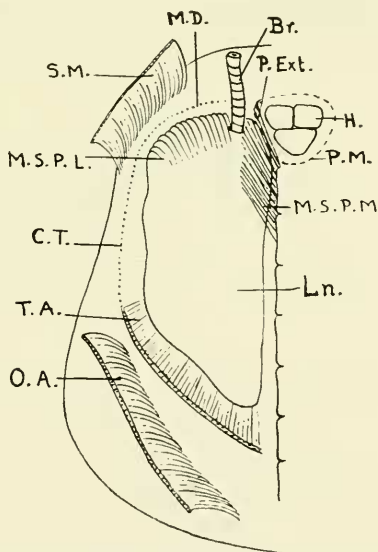


Fig. 11. Diagrammatic sketch of the disposition of the respiratory muscles in *Podocnemis*.

Six species belonging to the Testudininae, *Testudo hermanni*, *Testudo graeca*, *Geochelone pardalis*, *Testudo horsfieldii*, *Testudo kleinmanni* (Fig. 8) and *Pyxis arachnoides* (Fig. 9) have been examined. In all these except *Pyxis arachnoides* the *muscularis striatum pulmonale* is totally absent and a thin sheet of connective tissue is present in its place. In *Pyxis arachnoides* (Fig. 9) there is a poorly developed lateral part of the *muscularis striatum pulmonale* present, covering only a very small part of the anterior region of the lung. The presence of part of the

muscle in *Pyxis* appears to be a case of an intermediate stage between the typical condition of the Testudininae, on one hand, where the muscle is absent, and that of Emydinae, on the other, in which it is better developed.

In *Sternotherus odoratus* and *Sternotherus carinatus minor*, belonging to Kinosterninae, the *muscularis striatum pulmonale* is similar in its origin, course and insertion to that described for the *Malaclemys terrapin terrapin* (Fig. 3). In *Chelydra serpentina* of the Chelydrinae the muscle is completely absent and instead a thin layer of connective tissue is present in its place.

In *Chelonia mydas*, *Caretta caretta*, *Lepidochelys olivacea* and *Eretmochelys imbricata* (Fig. 7), which all belong to the family Chelonidae, the *muscularis striatum pulmonale* is totally absent. Even in *Dermochelys coriacea* (Fig. 7), of the Dermochelyoidea,

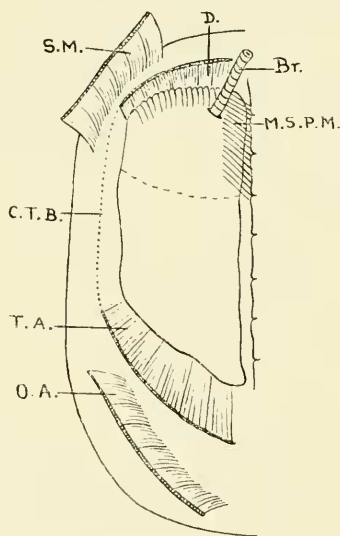


Fig. 12. Diagrammatic sketch of the disposition of the respiratory muscles in such Emydinae as *Geoemyda spinosa*, etc.

the muscle is absent. Thus, it appears that none of the marine forms possess any lung muscle, and that unlike the land forms or the fresh water ones there is no variation in this regard.

All the members belonging to the suborder Pleurodira possess a partial *muscularis striatum pulmonale* rather similar to that seen in the Emydinae (Fig. 5). The members of the genus

Podocnemis show an unusual extension of the *muscularis striatum pulmonale*. In *Podocnemis unifilis* and the other two species of *Podocnemis*, the medial part of the muscle, after its usual origin, runs forward adhering to the medial wall of the lung and (unlike the normal condition where the fibres terminate on the lung near the entrance of the bronchus) after reaching the anterior limit of the lung continues forward and closely adheres to the dorsolateral side of the pericardial membrane. Finally, these fibres insert on the membrane at the level of the anterior side of the auricles (Shah, in press). Such a pericardial extension of the *muscularis striatum pulmonale* is not found in any of the other pleurodirans that were studied. No trace of such an extension is present in any of the Cryptodira, nor does there appear to be any previous record of the presence of a striated muscle layer on the pericardium in any vertebrate.

FLANK CAVITY MUSCLES

The *diaphragmaticus* and the *transversus abdominis* form the expiratory set of the flank cavity muscles in Chelonia, while the *serratus magnus* and the *obliquus abdominis* form the inspiratory set (McCutcheon, 1943; George and Shah, 1954, 1958 and 1959).

In all Chelonia the *transversus abdominis* muscle is well developed. In the Cryptodira studied, the *transversus abdominis* muscle is the most highly developed in the Trionychoidea, and in this group it joins with the anteriorly placed *diaphragmaticus* muscle of the same side to form a continuous muscular sheath which envelops the visceral organs including the lungs. The muscle arises in all the chelonians from the posterior half of the carapace, but the place of origin is not constant in all forms since great variations in its extent are seen in different individuals. In *Pseudemys floridana* and *Pseudemys texana* the *transversus abdominis* muscle extends almost up to the level of the apex of the heart on the ventral side (Fig. 4). In no Emydinae, whether the *diaphragmaticus* muscle is present or not, does the *transversus abdominis* muscle have the extensive spread seen in all the Trionychoidea. In those Emydinae where the *diaphragmaticus* muscle is present, there is a bridge of connective tissue between it and the *transversus abdominis* of the same side. Such a bridge of connective tissue between the *diaphragmaticus* and the *transversus abdominis* muscle is present in all the species of the genus *Geoemyda* and all the marine chelonians.

The *diaphragmaticus* muscle, in all the chelonians in which it is present, arises from the undersurface of the second or third costal plates of the carapace. Its place of origin is oriented transversely with respect to the vertebral column. In all the forms of Trionychoidea (Figs. 1 and 2) the muscle is very highly developed and, as mentioned above, it joins the *transversus abdominis* muscle of its side to form a continuous muscular sheath to envelop the viscera. In some Emydinae the muscle is present (Fig. 12); in others it is absent (Figs. 3, 4, 5, and 6). No members of the Testudinae have the *diaphragmaticus* (Fig. 8); there is a thin layer of connective tissue in its place.

In all the chelonian studies the inspiratory muscles, the *severatus magnus* and the *obliquus abdominis* (Figs. 1 to 11), are present with such slight variation that these are not worth detailed discussion. On contraction of these muscles the volume of the body cavity is increased and thus a negative pressure is created in this cavity and so the lungs expand. On expansion of the lungs the atmospheric air rushes in and in this way inspiration is brought about.

DISCUSSION

From the present study of the respiratory muscles in Chelonia it is evident that there is a great deal of noticeable variation in two muscles, the *diaphragmaticus* and the *muscularis striatum pulmonale*. The variations in these two muscles range from a highly developed condition to a total absence, with all intermediate stages. The other respiratory muscles are always present, and although slight variations in different forms are seen, these are very minor ones.

The presence of the *muscularis striatum pulmonale* in all the Cyclanorbinac, where the muscle covers the lung completely, is regarded as a primitive character which is retained in these forms. The early ancestral chelonians presumably developed these muscles as a substitute for the intercostal muscles lost when their body wall was covered by the rigid shell and could not have the normal movements which are the main component of the respiratory mechanism in all other amniotes. The *muscularis striatum pulmonale* must thus have been of survival value to the early ancestral chelonians, and it is retained fully in all the Cyclanorbinac but shows a gradual trend toward total disappearance in other chelonians. Some chelonians, the Trionychinae, Testudinae and all the marine forms, have totally lost

this muscle. It is quite obvious that the presence of the muscle covering the lung is a hindrance to full expansion of the lungs; it must therefore have developed as a stop gap arrangement to tide over the loss of the body wall movements until some better physiological adaptation for respiration was achieved. Unpublished work by the author on the blood of some chelonians shows some interesting results. The oxiphoric capacity of the blood of *Lissemys punctata* where the *muscularis striatum pulmonale* covers the lungs completely is much less than that of the blood of *Trionyx* or *Testudo elegans* where the muscle is totally absent. The oxiphoric capacity of the blood of *Geoemyda trijuga*, where the *muscularis striatum pulmonale* muscle is incompletely developed (Fig. 12), shows intermediate values. Thus from the study of blood some light is thrown on the new physiological adaptations which have taken place, substituting for some of the morphological adaptations of the primitive forms. More work on the physiology of respiration in different chelonians will be necessary for a better understanding of the problem of respiratory mechanism in this order. Some aspects of this are being worked on at present in my laboratory at the University of Baroda.

ABBREVIATIONS USED IN FIGURES

Br.	Bronchus
C.T.	Connective tissue
C.T.B.	Bridge of connective tissues between <i>diaphragmaticus</i> and the <i>transversus abdominis</i> muscles.
D.	<i>Diaphragmaticus</i> muscle
H.	Heart
Ln.	Lung
M.D.	Connective tissue in place of the <i>diaphragmaticus</i> muscle.
M.S.P.	<i>Muscularis striatum pulmonale</i> muscle covering the left lung
M.S.P. ¹	<i>Muscularis striatum pulmonale</i> muscle cut horizontally and the right lung removed so as to show the place of origin of the muscle
M.S.P.L.	Lateral part of the <i>muscularis striatum pulmonale</i>
M.S.P.M.	Medial part of the <i>muscularis striatum pulmonale</i>
O.A.	<i>Obliquus abdominis</i> muscle
P.M.	Pericardial membrane
P. Ext.	Pericardial extension of <i>muscularis striatum pulmonale</i> .
S.M.	<i>Serratus magnus</i> muscle
T.A.	<i>Transversus abdominis</i> muscle

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